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RESEARCH PAPER

Biomes as evolutionary arenas: Convergence and conservatism in the trans-continental succulent biome

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Abstract

Aim: Historically, biomes have been defined based on their structurally and functionally similar vegetation, but there is debate about whether these similarities are superficial, and about how biomes are defined and mapped. We propose that combined assessment of evolutionary convergence of plant functional traits and phylogenetic biome conservatism provides a useful approach for characterizing biomes. We focus on the little-known succulent biome, a trans-continentally distributed assemblage of succulent-rich, drought-deciduous, fire-free forest, thicket and scrub vegetation as a useful exemplar biome to gain insights into these questions.

Location: Global lowland (sub)tropics.

Time period: Present.

Major taxa studied: Angiosperms.

Methods: We use a model ensemble approach to model the distribution of 884 species of stem succulents, a plant functional group representing a striking example of evolutionary convergence. Using this model, phylogenies, and species occurrence data, we quantify phylogenetic succulent biome conservatism for 10 non-succulent trans-continental plant clades including prominent elements of the succulent biome, representing over 800 species.

Results: The geographical and climatic distributions of stem succulents provide an objective and quantitative proxy for mapping the distribution of the succulent biome. High fractions of succulent biome occupancy across continents suggest all 10 non-succulent study clades are phylogenetically conserved within the succulent biome.

Main conclusions: The trans-continental succulent and savanna biomes both show evolutionary convergence in key biome-related plant functional traits. However, in contrast to the savanna biome, which was apparently assembled via repeated local recruitment of lineages via biome shifts from adjacent biomes within continents, the succulent biome forms a coherent trans-continental evolutionary arena for drought-adapted tropical biome conserved lineages. Recognizing the important functional differences between the succulent-rich, grass-poor, fire-free succulent biome and the grass-dominated, succulent-poor, fire-prone savanna biome, and defining them

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as distinct seasonally dry tropical biomes, occupying essentially non-overlapping distributions, provides critical insights into tropical biodiversity and the extent of biome stasis versus biome shifting.

KEYWORDS

biome definition, evolutionary arena, evolutionary convergence, lowland tropics, phylogenetic biome conservatism, stem succulence, succulent biome, trans-continental disjunction

1 | INTRODUCTION

Biomes have been defined as 'globally distributed, structurally and functionally similar vegetation units' (Moncrieff, Bond, & Higgins, 2016), but the significance of these similarities remains much debated. Some have argued that geographically disjunct areas of the same biome are ecologically and evolutionarily independent, and that any similarity is merely superficial (Corlett & Primack, 2006). Others consider biomes to represent coherent evolutionary arenas (*sensu* Nürk et al., 2019) with distinct histories and biotic and abiotic characteristics that shape and confine the evolution and distribution of the lineages inhabiting them (Eiserhardt, Couvreur, & Baker, 2017; Hughes, Pennington, & Antonelli, 2013; Moncrieff et al., 2016; Pennington, Lavin, & Oliveira-Filho, 2009; Pennington, Lehmann, & Rowland, 2018). Detailed analyses of the lineages composing a biome can help to distinguish between these two contrasting hypotheses. If biomes coincide with distinct evolutionary arenas, due to similar selection pressures and a partially shared history, disjunct regions of the same biome should share functional traits and functional groups, that is, show a strong signal of evolutionary convergence across distantly related lineages. If this is the case, these functional traits could also play an important role in defining and mapping biomes. In addition, geographically disjunct regions of a biome should also share evolutionary lineages exhibiting phylogenetic biome conservatism, that is, lineages made up of species that retain ancestral ecological traits and environmental distributions (Crisp et al., 2009; Donoghue & Edwards, 2014), and that are significantly confined within a biome by strong adaptive barriers, but trans-continentally distributed across its distribution. While striking examples of large-scale phylogenetic biome conservatism have been demonstrated (e.g. Crisp et al., 2009; Donoghue, 2008; Lavin et al., 2004; Segovia et al., 2019), the overall extent and prevalence of phylogenetic biome conservatism versus biome shifting remain debatable (Donoghue & Edwards, 2014; Edwards & Donoghue, 2013). Here we investigate these two important attributes of biomes, evolutionary convergence and phylogenetic conservatism, to test to what extent biomes can be considered as distinct evolutionary arenas.

Quantifying phylogenetic biome conservatism and the convergence of traits within a biome depends on how biomes are defined and mapped, but there is no universally accepted framework for this (Higgins, Buitenwerf, & Moncrieff, 2016; Moncrieff et al., 2016), nor is there a general agreement about the number and location of tropical biomes. As pointed out by Dexter et al. (2018) and setting aside true

deserts, most research on tropical biodiversity divides the vegetation of the lowland tropics into two broad categories: rain forests and savannas, or forest versus 'open' vegetation (Antonelli et al., 2018; Oliveras & Malhi, 2016; Staver, Archibald, & Levin, 2011). Savannas are found in areas with a pronounced dry season and abundant C_4 grasses, and are prone to regular fires (Lehmann et al., 2019; Lehmann & Parr, 2016). Rain forests, in contrast, receive year-round precipitation, have few grasses, and do not experience fire (Eiserhardt et al., 2017). However, a third major lowland tropical biome, the seasonally dry, drought-deciduous, but grass-poor and fire-free vegetation referred to as the succulent biome *sensu* Schrire, Lavin, and Lewis, 2005, has been recognized (Dexter et al., 2018; Gagnon, Ringelberg, Bruneau, Lewis, & Hughes, 2019; Lavin et al., 2004; Oliveira-Filho et al., 2013; Schrire et al., 2005), but remains little known, lacks a quantitative distribution map, and is often neglected.

Despite this neglect, the succulent biome includes important hotspots of endemism (DRYFLOR, 2016; Marshall, Wieringa, & Hawthorne, 2016), most notably in Africa, where the hottest hotspots of range-restricted plant endemism are in the succulent biome (Marshall et al., 2016). The succulent biome is thus a high conservation priority, yet large portions of it are threatened (DRYFLOR, 2016; Kuemmerle et al., 2017; Pennington et al., 2018), and neglected as conservation priorities compared to rain forests (Pennington et al., 2018). Ignorance of the succulent biome is also evident in many prominent recent studies investigating assembly of tropical diversity (e.g. Antonelli et al., 2018; Charles-Dominique et al., 2016), which often conflate the succulent biome with the climatically similar but functionally distinct savanna biome. There is thus a clear need for an objective quantitative map of the succulent biome, and a better understanding of the differences between the succulent and savanna biomes (Pennington et al., 2018).

A defining characteristic of the succulent biome is the presence of large stem succulents, that is, plants over 1 m height with stems containing specialized water-storing tissue. This functional plant group distinguishes the succulent biome from savannas and rain forests. Savannas dominated by C_4 grasses experience regular fires with most savanna species adapted to tolerate or resist fire (Maurin et al., 2014; Ratnam et al., 2011; Simon et al., 2009). Stem succulents are notably vulnerable to fire (Cousins & Witkowski, 2012; Moe, Møbæk, & Narmo, 2009; Thomas, 1991) and almost absent from savannas. Similarly, in rain forests stem succulent species are also typically absent. Stem succulence is a textbook example of evolutionary convergence, occurring in over 20 plant families (Ávila-Lovera &

Ezcurra, 2016; Egli & Nyffeler, 2009; Griffiths & Males, 2017; Ogburn & Edwards, 2010), and occupying a highly disjunct distribution across the tropics (Ávila-Lovera & Ezcurra, 2016; Ellenberg, 1981; Ogburn & Edwards, 2010).

Here we investigate the combination of evolutionary convergence of plant functional traits and phylogenetic conservatism of lineages as a way to test the hypothesis that biomes can be defined and characterized as evolutionary arenas. We focus on the neglected and little-known succulent biome as a particularly suitable system to test this hypothesis, because it occupies a highly disjunct, trans-continental distribution. We generate an objective, quantitative global map of this biome to test the hypotheses that (a) the distribution of large stem succulent plant species, a prominent example of evolutionary convergence, is a good proxy for the distribution of the succulent biome, and (b) multiple non-succulent angiosperm clades that include common and dominant species in the succulent biome are phylogenetically conserved across this biome.

2 | METHODS

Data handling and analyses were performed in R versions 3.3.2–3.6.0 (R Core Team, 2018).

2.1 | Stem succulent modelling

2.1.1 | Stem succulent occurrence data

We assembled a checklist of accepted names and synonyms of 1,120 succulent species listed in several encyclopaedic compendia (Albers & Meve, 2004; Anderson, 2001; Egli, 2001, 2004). We defined stem succulents as plants with stems containing specialized water-storing tissue, including pachycaul species [e.g. *Ceiba insignis* (Malvaceae)] and arborescent/caulescent giant-leaf succulents [e.g. *Aloe dichotoma* (Asphodelaceae)]. As climbing, clambering, pendant, epiphytic and shrubby (<1 m tall) succulent species do not form structural components of vegetation indicative of fire-free ecologies and are more likely to occur in azonal areas and atypical climates, these species were excluded.

We downloaded occurrence records from the Global Biodiversity Facility (GBIF; www.gbif.org; see Supporting Information Table S1 for DOIs), the Latin American Seasonally Dry Tropical Forest Floristic Network (DryFlor; <http://www.dryflor.info>) and the Southwestern Environmental Information Network (<http://swbiodiversity.org/seinet>). For c. 200 species on the checklist no occurrence data were available. We performed extensive data cleaning, assigning synonyms to their accepted names, and removing records not based on vouchered herbarium collections, those with imprecise coordinates (i.e. only degrees, no minutes or seconds), located in the sea, or occurring outside the known distributions of species given by Albers and Meve (2004); Anderson (2001); Egli (2001, 2004), plus cultivated records and country centroids.

Four stem succulent richness maps were generated: one by counting the number of unique genera per 0.25° lat./long. grid cell, two by varying the grid cell sizes to 0.1° and 0.5°, and one by counting unique species rather than genera. Since the global distribution of stem succulent richness on these maps was strongly influenced by the spatial sampling bias of the GBIF data (Meyer, Weigelt, & Kreft, 2016; which accounted for c. 75% of the data), we modelled the distribution of stem succulents, rather than using it directly in further analyses. The four richness maps were used to generate four independent models, but since the results are highly similar (Supporting Information Figures S1–S4), we discuss the methods and results in detail only for the 0.25° genus map.

2.1.2 | Predictor variables

Twenty-two climatic and topographic predictor variables were obtained from climatologies at high resolution for the earth's land surface areas (CHELSA) 1.2 (Karger et al., 2017), WorldClim 2.0 (Fick & Hijmans, 2017) and EarthEnv.org (Amatulli et al., 2018; Wilson & Jetz, 2016) (Supporting Information Table S2), and aggregated to the same spatial resolution as the stem succulent richness maps using the 'mean' option of the aggregate function of the 'raster' package (Hijmans, 2018). In order to avoid multicollinearity problems when fitting models, we reduced the number of predictor variables by calculating variance inflation factors (VIFs) and Pearson's correlations between all predictors, removing those with VIFs ≥ 7 and correlations ≥ 0.7 , which resulted in 13 predictors being retained (Supporting Information Table S3).

2.1.3 | Distribution modelling

We first produced a global model using all stem succulent occurrence points (Supporting Information Figure S5). However, this model yielded a poor match with the occurrence data in several areas, such as the Sahara and Saudi Arabia. Therefore, we decided to model the distribution of stem succulents separately for the New World and the Old World (Africa, Madagascar and Arabia). We extracted presence points from the stem succulent richness map at two levels of richness, i.e., with at least two or three unique genera per grid cell. This resulted in 2,210 and 1,270 presence points, respectively, for the New World and 640 and 256 presence points for the Old World. For the whole of Australia and Asia, there were only five and zero presence points, which we deemed to be too few to model properly.

We used a model ensemble approach to map the spatial distribution of stem succulents (Thuiller, Lafourcade, Engler, & Araújo, 2009), selecting: (a) a generalized linear model (GLM), (b) a generalized additive model (GAM), and (c) a random forest (RF). By combining these three methods, different degrees of model complexity are incorporated (Merow et al., 2014). See Supporting Information for details.

We used two different regions (the New World and the Old World), two different levels of determining presence data (two and three genera per grid cell), three different models (GLM, GAM and RF), and two different thresholds (optimizing Kappa and true skill statistic), generating a total of 24 unique models. The final map of the occurrence of stem succulents was created by combining all 12 unique binary output maps for each region.

The few grid cells that were not deemed suitable for stem succulents by the models but did contain at least two observed genera were manually assigned as presence. For the assignment of species to the succulent biome (see below), the continuous stem succulents map was converted to binary with a threshold of 33% (partially following Chala et al., 2016).

2.2 | Succulent biome conservatism

2.2.1 | Study clades

We identified 10 non-succulent amphi-Atlantic plant clades as abundant and prominent elements in the succulent biome, some from previous studies (Gagnon et al., 2019; Lavin et al., 2004; Thiv et al., 2011). With the exception of 16 species of *Bursera* and *Commiphora*, none of the species of these clades was used for generating the stem succulents map. Per clade we assembled a taxonomic checklist (see Supporting Information) and occurrence data set using the same approach as for the stem succulents (Supporting Information Table S1). All species with over half of their occurrences co-occurring with stem succulents (omitting multiple occurrences of the same species at the same location) were assigned to the succulent biome, and remaining species were assigned to savanna, rain forest, temperate or coastal biomes, based on their distribution and habitat information. Biome assignments based on the four different biome modelling approaches were highly similar (Supporting Information Figure S6). In some cases, species were assigned to more than one biome, and in rare cases, species with over half their occurrences in the succulent biome were assigned to a different biome (11 out of 839 total species), or vice versa (18 species), based on expert knowledge.

2.2.2 | Phylogeny reconstruction

Phylogenies from each study clade were obtained either by downloading previously generated phylogenies, or by inferring them using published molecular data. See Supporting Information for details.

2.2.3 | Phylogenetic biome conservatism

Several of our study clades are trans-continentially distributed yet (almost) completely restricted to the succulent biome, providing definitive evidence of phylogenetic succulent biome conservatism, and precluding the need for any formal tests. For the remaining clades we

tested for biome conservatism using the same approaches as Gagnon et al. (2019): comparing the total number of biome shifts to a null distribution, and measuring phylogenetic signal. Biome shifts were assessed with stochastic character mapping using the `make.simmap` function of the 'phytools' package (Revell, 2012), run for 200 simulations under equal rates (ER) and symmetrical (SYM) models, and compared to numbers of shifts obtained by re-running `make.simmap` 99 times with randomized tip states. An observed number of biome shifts that falls within the lowest 5% of biome shifts obtained from the randomized distribution is considered evidence for conservatism (Maddison & Slatkin, 1991). Phylogenetic signal was quantified using the `fitDiscrete` function of the 'geiger' package (Harmon, Weir, Brock, Glor, & Challenger, 2008), which measures Pagel's lambda (Pagel, 1999). Before running `fitDiscrete` the optimal character evolution model [ER, SYM or all rates different (ARD)] for each clade was determined using 'phytools' `fitMk` function. Some phylogenies contained polytomies, which were randomly resolved 10 different times using the `multi2di` function of the 'ape' package (Paradis & Schliep, 2019), creating a set of fully resolved trees. As `fitDiscrete` does not allow polymorphic character states, in clades with species assigned to more than one biome phylogenetic signal was determined separately for each possible combination of biome states for polymorphic species (with the exception of the *Caesalpinia* group, where the total number of combinations was very large, and `fitDiscrete` was run for 100 randomly selected combinations of polymorphic biome states instead). For clades with sets of trees, sets of possible biome states, or both, the median phylogenetic signal was calculated. High phylogenetic signal was interpreted as an indication of conservatism (but see Losos, 2008; Revell, Harmon, & Collar, 2008).

3 | RESULTS

3.1 | Stem succulent modelling

We obtained 47,575 quality-controlled occurrence points for 884 species and infraspecific taxa of stem succulents, from 102 genera and 22 families (Supporting Information Table S4). Different modelling methods and ways of counting presences yielded highly consistent results (Supporting Information Figures S1–S4 and Table S3). The combined analysis of 24 unique models showing the distribution of stem succulents (Figure 1) is consistent with previous studies (Ávila-Lovera & Ezcurra, 2016; Ellenberg, 1981; Ogburn & Edwards, 2010), and, with some notable exceptions, closely matches the distribution of the succulent biome depicted by Schrire et al. (2005).

Climatically, the distribution of grid cells containing at least two genera of stem succulents closely matches the proposed climate of the succulent biome (Dexter et al., 2018; Oliveira-Filho et al., 2013; Schrire et al., 2005; Silva de Miranda et al., 2018; Figure 2). Ninety percent of cells containing stem succulents receive less than 1,300 mm annual precipitation, close to the 1,200 mm upper limit for succulent biome in eastern South America proposed by Oliveira-Filho et al. (2013) (Figure 2d). The climatic overlap between New and

Old World succulents is high (Figure 2a), in contrast to the markedly incomplete climatic overlap between savannas on different continents (Lehmann et al., 2014) and across biomes on different

continents in general (Moncrieff, Hickler, & Higgins, 2015). The only exception to the pattern of overlap is that some New World succulents occur at higher elevations (Figure 2b), while some Old World

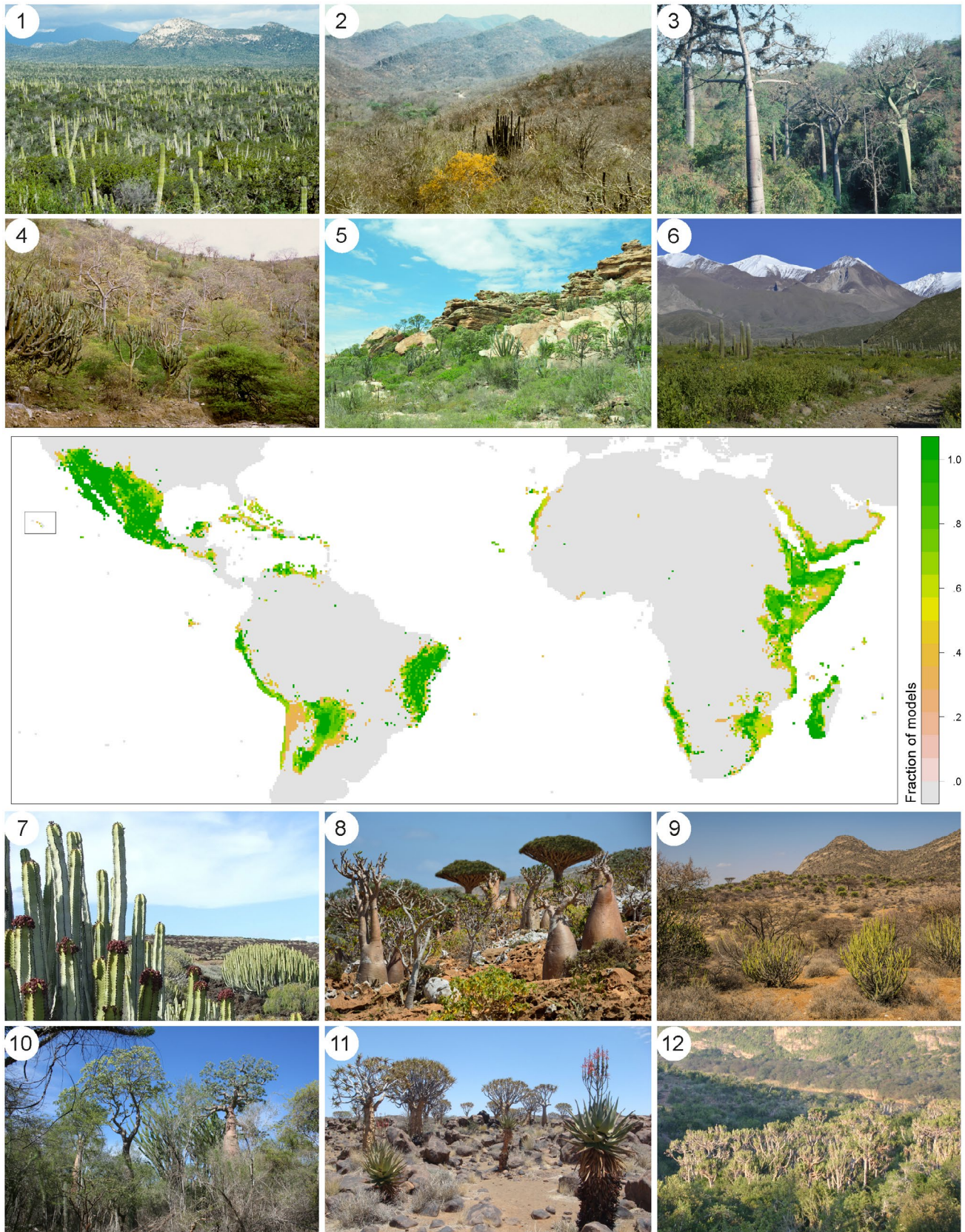


FIGURE 1 The trans-continental distribution of the succulent biome. Map showing the modelled probability distribution of stem succulents, averaged over 24 unique models (see Methods) with a cut-off at a minimum probability of occurrence of 33%. Colours on the map correspond to fraction of models predicting the occurrence of stem succulents in each grid cell. The inset shows Hawai'i. The distribution of stem succulents provides a proxy for the distribution of the succulent biome. The full global map showing the absence of stem succulents from most of Asia and Australia is in Supporting Information Figure S1. Images provide an overview of the vegetation, landscapes, and stem succulent species and growth forms that make up the succulent biome, illustrating both the convergent evolution of stem succulence, the key plant functional type defining this biome, and variation in stature and vegetation cover ranging from scrub and thicket vegetation with an open cover of small trees and shrubs, to closed deciduous seasonally dry tropical forest (SDTF). All these vegetation types are notably poor in grasses, rich in stem succulents and fire-free, a set of characteristics that distinguishes the succulent from the savanna biome: (1) Baja California, Mexico, cactus-rich dry thorn scrub; (2) Pacific coastal Oaxaca, Mexico, SDTF; (3) Loja province, southern Ecuador, pachycaul Malvaceae in SDTF; (4) the inter-Andean Marañón Valley, Peru, SDTF; (5) north-east Brazil, Caatinga vegetation (cactus-rich dry thorn scrub); (6) northern Argentina, dry thorn scrub with Cactaceae; (7) Tenerife, Canary Islands, Spain, tabaibal-cardonal (coastal succulent scrub) with *Euphorbia canariensis* (Euphorbiaceae); (8) Socotra, Yemen, succulent shrubland with *Adenium obesum* subsp. *socotranum* (Apocynaceae) and *Dracaena cinnabari* (Ruscaceae); (9) northern Kenya, Somali-Masai *Acacia-Commiphora* woodland with *Euphorbia atroflorea* and *Euphorbia magnicapsula* subsp. *lacertosa*; (10) south-west Madagascar, spiny forest; (11) southern Namibia, desert scrub with *Aloe dichotoma* and *Aloe littoralis* (Asphodelaceae); (12) Eastern Cape, South Africa, succulent thicket vegetation with *Euphorbia tetragona*. Photos courtesy of: 1, 2 & 4 Colin Hughes, 3 Gwilym Lewis, 5 Domingos Cardoso, 6 Edeline Gagnon, 7 Mark Carine, 8 Luciano Napolitano (<http://www.travel-tour-guide.com>), 9 Frans Noltee (<http://enjoysucculents.com>), 10 Andrea Weeks, 11 Roman Kellenberger, 12 Richard Cowling

succulents occur in areas that are slightly warmer, with higher solar radiation and evapotranspiration rates. In addition, occurrences of succulent biome extend further into the Northern Hemisphere in the New World (Supporting Information Figure S11), and overall the biome shows an intriguing bimodal latitudinal distribution concentrated mainly between 10° and 30° north and south of the equator, presenting an exception to the general latitudinal diversity gradient.

3.2 | Succulent biome conservatism

Using occurrence data (83,373 records for 839 species; Figure 3) and our newly generated map we quantified the extent to which species of 10 non-succulent amphi-Atlantic plant clades can be assigned to the succulent biome to assess phylogenetic succulent biome conservatism (Table 1). A high fraction of succulent biome occupancy combined with a trans-continental distribution provides strong evidence for biome conservatism. For example, *Bursera* is a ubiquitous, abundant and often dominant tree in Mexican seasonally dry tropical forests (SDTFs; De-Nova et al., 2012), while its sister group, the genus *Commiphora*, is equally abundant in dry parts of Africa and Madagascar, lending its name to the *Acacia-Commiphora* woodlands of the Somali-Masai region (Supporting Information Figure S14) (Gostel, Phillipson, & Weeks, 2016; White, 1983). Ninety-three percent of the c. 235 species in the *Bursera-Commiphora* clade are confined to the succulent biome across continents and there are two trans-Atlantic disjunctions spanning areas of succulent biome within this clade (Table 1, Figure 3 and Supporting Information Figures S14 and S15). Similarly, *Parkinsonia* and *Delonix* are common and conspicuous trees in dry parts of the Neotropics (Pérez-García, Meave, & Cevallos-Ferriz, 2012) and the dry spiny forests of Madagascar (Babineau & Bruneau, 2017), respectively (Supporting Information Figure S22), and all 27 species of the *Parkinsonia-Delonix* clade are restricted to the succulent biome, again with two separate succulent biome trans-Atlantic disjunctions (Table 1, Figure 3 and Supporting Information

Figures S22 and S23). This high trans-continental succulent biome occupancy applies to six of the study clades, each with over 85% of its species in the succulent biome. While the remaining four clades have relatively fewer species in this biome, they still show moderate to high levels of succulent biome conservatism, as indicated by a high phylogenetic signal and a low number of biome shifts compared to a randomized biome distribution (Gagnon et al., 2019; Table 1). Many other plant and some animal clades also appear to show striking succulent biome conservatism (Supporting Information Table S5).

4 | DISCUSSION

4.1 | Biome mapping

The occurrence of functionally and structurally similar but geographically disjunct and floristically distinct vegetation formations was first noted by von Humboldt over 200 years ago, and biomes have played a prominent role in ecology, evolution and biogeography ever since (Moncrieff et al., 2016; Mucina, 2019). However, there is controversy about how biomes are defined and mapped (Higgins et al., 2016; Moncrieff et al., 2016; Mucina, 2019). Most biome maps are based on combinations of climatic data, existing vegetation maps and expert opinion (Olson et al., 2001), or remotely sensed vegetation types (Friedl et al., 2010). Here we use a different approach, by mapping a key plant functional group. Existing biome maps that explicitly take into account functionality are based on mechanistic models (Prentice et al., 1992), regressions of trait observations against climate (van Bodegom, Douma, & Verheijen, 2014), or remotely sensed broad functional types (Higgins et al., 2016). Our method is markedly different: by identifying (practically) all species that make up the functional group known as stem succulents, mapping these species-by-species and quantifying global richness patterns, we use a bottom-up approach to biome mapping. This approach has two advantages. First, although here performed on a

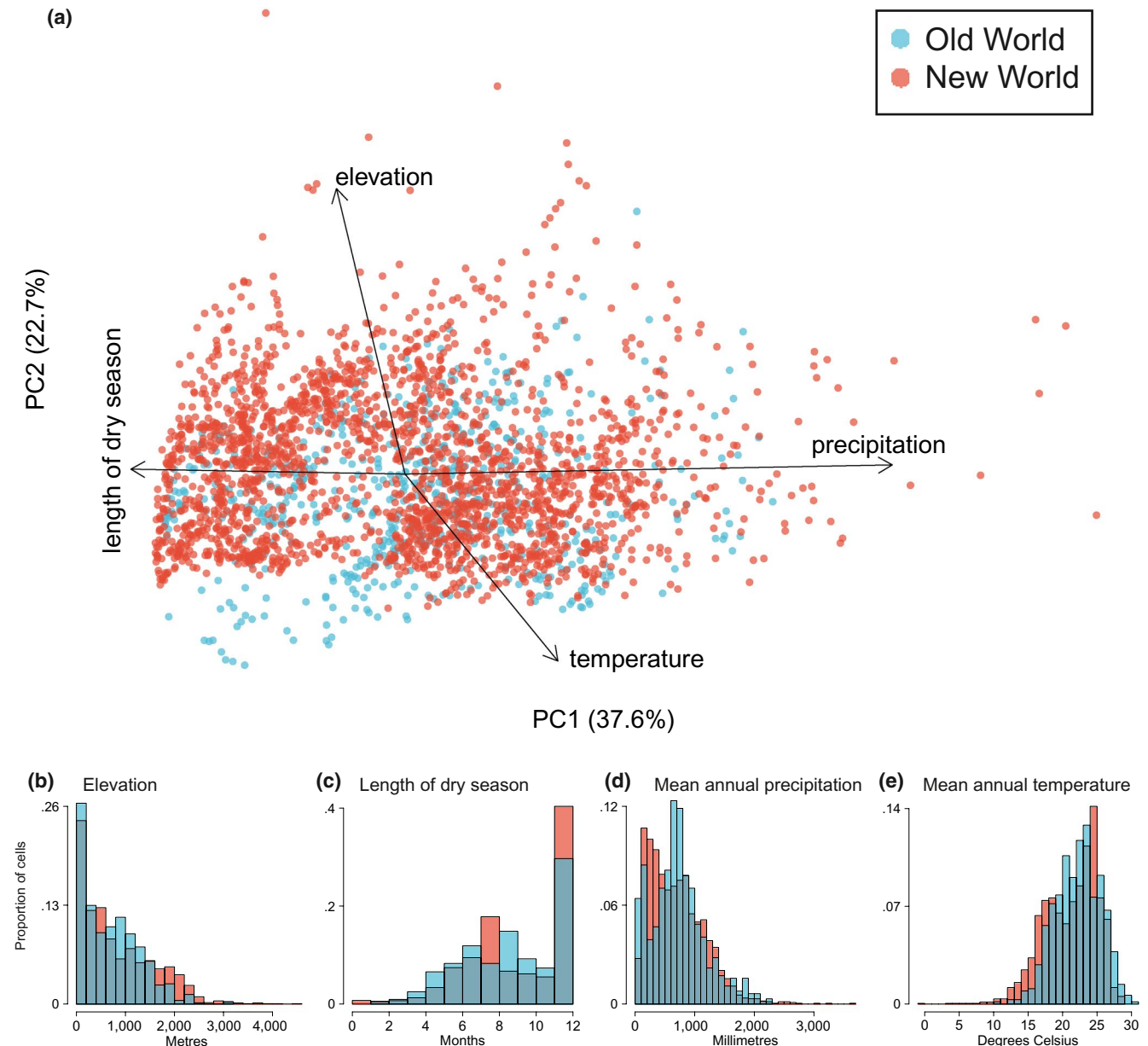


FIGURE 2 Climate of the succulent biome. Subfigures depict climatic values of all 2,850 0.25° lat./long. grid cells with at least two unique stem succulent genera (see Methods). (a) Principal components analysis (PCA) showing the high climatic overlap between the succulent biome in the New and Old Worlds. Arrows indicate direction, but not magnitude, of the same four climatic variables depicted in b–e. See Supporting Information Figure S9 for a PCA depicting all climatic variables used in this study. (b) Elevational distribution of the succulent biome. (c) Length of the dry season (consecutive months with rainfall < 100 mm/month). Over half of all cells have a dry season of at least 10 months. (d) Distribution of mean annual rainfall, which closely matches that of South American seasonally dry tropical forests (SDTFs) (Dexter et al., 2018: their fig. 2), except that stem succulents also occur in drier areas. (e) Mean annual temperature distribution, showing that the succulent biome mainly occurs in frost free areas (also see Supporting Information Figure S10)

global scale, if species occurrence data are densely sampled, there is no reason this approach cannot work on more local scales to produce a higher resolution map that more accurately reveals the local interdigitation of biomes in parts of Mexico and south-east Africa where the succulent biome is currently over-projected (see below). Second, this method could be used for any functional trait. This is not to imply that every functional trait is a proxy for a unique biome, but simply that global maps of key functional traits would be very

insightful for defining and mapping biomes (Moncrieff et al., 2016). Possibilities might include high-resolution global maps of crassulacean acid metabolism photosynthesis, annual versus perennial plant life history, plant growth forms including lianas and geoxyles, C_4 grasses, leaves with drip tips, sclerophyly, deciduousness and spinescence; there are many options. A complication with this approach is spatial biases in available species occurrence data (Meyer et al., 2016), but as we show, this problem can be circumvented by

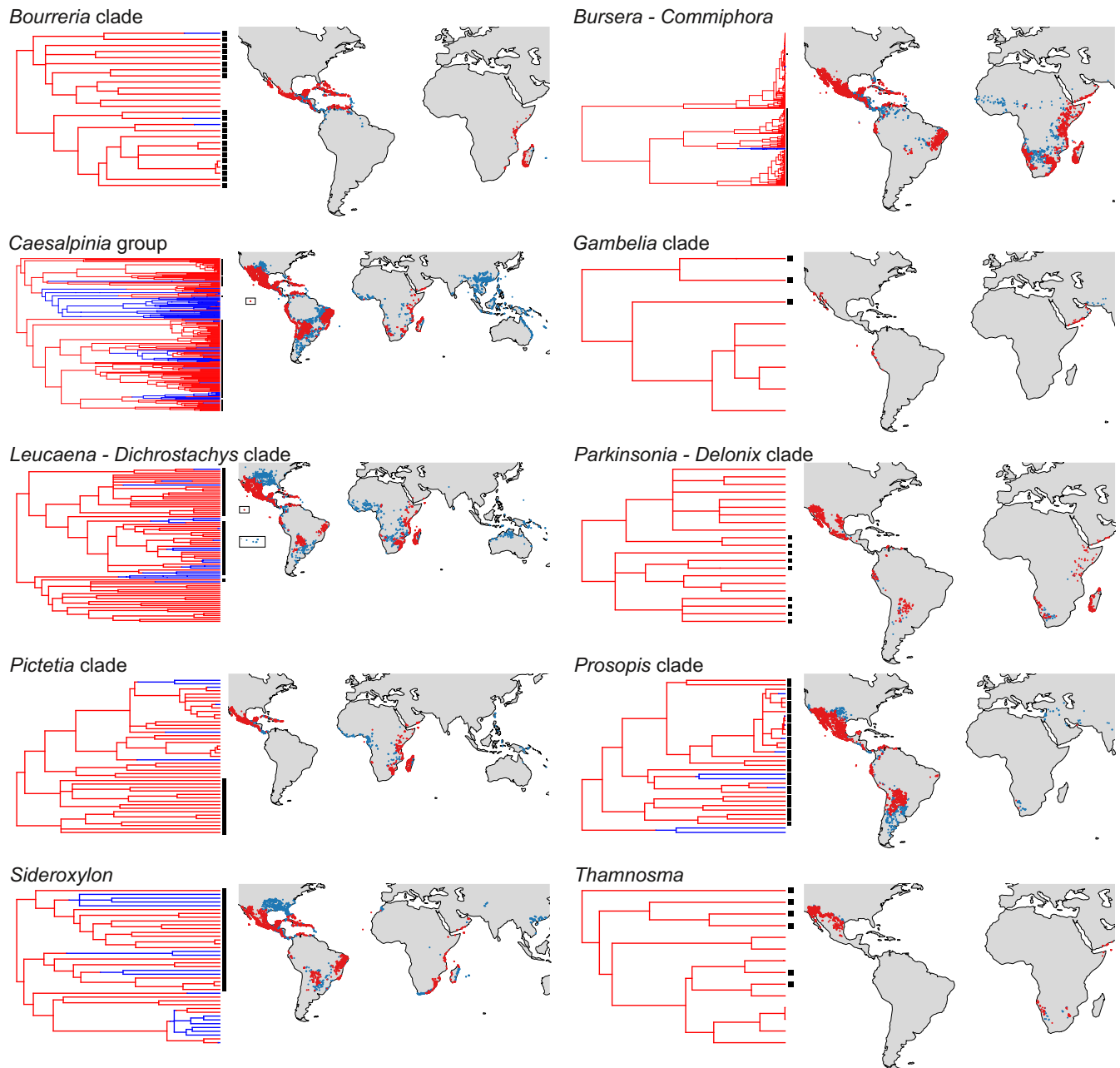


FIGURE 3 Phylogenies, geographical distributions and succulent biome occupancy for 10 non-succulent angiosperm clades. On the maps and phylogenies, red corresponds to species/occurrences in the succulent biome, and blue in other biomes. Black squares on the tips of the phylogenies indicate New World species, absence of a square indicates Old World. Branches of the phylogenies are coloured based on the biome optimizations (see Methods). The insets on the maps of the *Caesalpinia* group and the *Leucaena-Dichrostachys* clade show Hawai'i and several islands in the South Pacific Ocean. Detailed phylogenies with terminal names and larger sized distribution maps are in Supporting Information Figures S12–S31

species distribution modelling, and occurrence data are rapidly expanding. A logical next step would be to map not just occurrences of functional traits, but also their abundance, based on global plot data (Oliveira-Filho et al., 2013).

While we are confident that the output of our models (Figure 1) accurately depicts the global distribution of stem succulents, an important caveat is that stem succulents do not necessarily occur at every location predicted by our model, nor do we claim they are absent from all areas not predicted by our

model. First, there is a trade-off between specificity and generality, most notably in the spatial scale of the modelling. While our selected scale (0.25° long./lat. grid cells) is not that coarse, there is still scope for heterogeneity within cells deemed uniform by the model. Second, stem succulents can occur on azonal landscape features such as inselbergs, termitaria (Moe et al., 2009), and rocky outcrops that are less fire-prone than surrounding savannas (Cousins & Witkowski, 2012; Pérez-García et al., 2012; Thomas, 1991). Third, while much digitized species occurrence

TABLE 1 Non-succulent angiosperm study clades and results of the phylogenetic biome conservatism tests

Clade	Species in clade (fraction in succulent biome)	Species in phylogeny (fraction in succulent biome)	Biome shifts significantly lower than random?	Phylogenetic signal	Trans-Atlantic disjunctions (fraction in succulent biome)
<i>Bourreria</i> clade (Ehretiaceae)	56 (.88)	26 (.88)	No	1	1 (1.00)
<i>Bursera–Commiphora</i> (Burseraceae)	235 (.93)	181 (.96)	No	.99	2 (1.00)
<i>Caesalpinia</i> group (Leguminosae)	199 (.68)	175 (.73)	Yes	.83	7 (.71)
<i>Gambelia</i> clade (Plantaginaceae)	11 (.91)	8 (.88)	–	–	1 (1.00)
<i>Leucaena–Dichrostachys</i> clade (Leguminosae)	100 (.79)	78 (.78)	Yes	.76	2 (1.00)
<i>Parkinsonia–Delonix</i> clade (Leguminosae)	27 (1.00)	21 (1.00)	–	–	2 (1.00)
<i>Pictetia</i> clade (Leguminosae)	52 (.87)	45 (.87)	Yes	.48	1 (1.00)
<i>Prosopis</i> clade (Leguminosae)	61 (.70)	35 (.69)	No	1	1 (1.00)
<i>Sideroxylon</i> (Sapotaceae)	87 (.59)	41 (.59)	Yes	.99	1 (1.00)
<i>Thamnosma</i> (Rutaceae)	11 (1.00)	14 (1.00)	–	–	1 (1.00)

Note: The second column only lists the number of species per clade for which occurrence data are available; some clades contain more species in total than are listed. The fractions of succulent biome occupancy reflect species exclusively occurring in the succulent biome, not species occurring in the succulent biome in addition to a different biome.

data are available, some regions, such as India and north-east Africa, are significantly under-represented (Meyer et al., 2016). Finally, a handful of stem succulents (c. 15 species) are known from more mesic areas outside of the succulent biome, perhaps reflecting the difficulties associated with how to define succulents in general, and stem succulents in particular (Eggli & Nyffeler, 2009; Ogburn & Edwards, 2010). These factors probably explain why, although highly consistent on a global scale, locally there are minor differences among the four stem succulent maps (Supporting Information Figures S1–S4), and also likely play a role in the apparent over-projection in Mexico (see below). Despite these minor shortcomings, the map of the global distribution of stem succulents is as accurate and detailed as is possible based on available data, and provides a useful quantitative global map of the succulent biome for macroevolutionary studies.

4.2 | The trans-continental succulent biome

In the New World, the distribution of stem succulents includes all areas of SDTF (DRYFLOR, 2016; Pennington et al., 2009; Pennington, Prado, & Pendry, 2000) in the Brazilian Caatinga, the Bolivian Chiquitania, Piedmont in Argentina, dry inter-Andean valleys, semi-arid coastal zones of Colombia and Venezuela, and dry forests in the Caribbean, Central America and Mexico (Figure 1). However, stem succulents have a broader range than SDTFs, extending into drier areas in northern Mexico and the arid coasts of Peru and Chile. When the distribution of stem succulents is modelled separately for occurrences with mean annual precipitation above and below 1,000 mm, the > 1,000 mm 'wetter' model (Supporting Information Figure S7) more closely resembles the typical distribution of SDTFs (DRYFLOR, 2016; Pennington et al., 2000). In contrast, most New World stem succulent occurrences fall into the 'drier' < 1,000 mm category, and this model maps the more arid areas of the New World (Supporting Information Figure S7), including the Caatinga, even though this is usually considered typical SDTF (de Queiroz, Cardoso, Fernandes, & Moro, 2017). While SDTFs span a range of precipitation (Dexter et al., 2018; Pennington et al., 2009), our results suggest that typical SDTFs occur mainly across the wetter portion of the succulent biome, which overall also encompasses more arid scrub and thickets, but always with a more or less open cover of deciduous shrubs, small trees, and stem succulents. In Mexico the taxonomic affinities of the arid northern deserts to wetter southern SDTFs (Pérez-García et al., 2012) fit with this wider definition of the succulent biome, as does the modified descriptor SDTFW ('SDTF and Woodland') suggested by de Queiroz et al. (2017). Nevertheless, our model appears to over-project succulents to areas where they are less abundant in mid-elevation pine-oak forests in Mexico. This is a function of the wide ecological, geographical and altitudinal amplitude of stem succulents, and especially Cactaceae, in the New World, as well as the small-scale interdigitation of the succulent biome with these climatically similar pine-oak forests.

Another discrepancy between our stem succulent model and traditional SDTF maps is the Chaco. The Chaco has characteristics of SDTFs (seasonally dry, fire-free, grass-poor), is clearly not a savanna, as indicated in the latest global map of grassy biomes (Lehmann et al., 2019), appears to comprise a mosaic of elements from several biomes (Segovia et al., 2019), and has been considered a distinct biome based on differences in soils, occurrence of frost, and floristic composition (DRYFLOR, 2017; Pennington et al., 2000; Silva de Miranda et al., 2018). The affinities of the Chaco remain debatable (Kuemmerle et al., 2017; Segovia et al., 2019). Twenty-three species of stem succulents occur in the Chaco, some of them endemic there, and the Chaco is clearly included in our succulent biome model (Figure 1). While this does not mean the Chaco is a typical SDTF, based on occurrence of stem succulents, the Chaco and other Neotropical SDTFs cannot be distinguished.

In the Old World, the major centres of stem succulent diversity are in the northern succulent Karoo, the Namib desert, and the *Acacia-Commiphora* woodlands of the Somali-Masai region in Africa, western Madagascar (spiny forests in the south and deciduous forests in the north), and coastal Arabia (Figure 1). The distribution in continental Africa closely matches the Arid Corridor (De Winter, 1971; Poynton, 1995) or Arid Flora (Linder, 2014), well known for its many disjunctly distributed taxa (De Winter, 1971; Jürgens, 1997; Linder, 2014; Poynton, 1995; Thiv et al., 2011). The most important differences between our model and the map of Schrire et al. (2005) are in south-east Africa. Coastal subtropical thicket vegetation of the Eastern Cape of South Africa has a notable presence of stem succulents (Figure 1), and is included in the succulent biome (Cowling, Procheş, & Vlok, 2005; Linder, 2014). Our stem succulent model also extends into inland areas of south-east Africa generally not considered part of the coastal thicket vegetation [although they feature Arid Corridor disjunctions (Jürgens, 1997; Poynton, 1995; Thiv et al., 2011)]. This region contains many stem succulent Apocynaceae, Asphodelaceae, Euphorbiaceae and Malvaceae, but is also characterized by the presence of C_4 grasses and regular fires and generally classified as savanna (White, 1983). We suggest that stem succulents in this area occupy locally fire-free azonal sites (rocky gullies and outcrops and termitaria; Cousins & Witkowski, 2012; Moe et al., 2009), with a mosaic of pockets of succulent biome across a region of predominantly savanna. The other discrepancy with Schrire et al. (2005)'s map is that our model does not predict stem succulents in coastal Iran, Pakistan and northwest India due to lack of occurrence data (Supporting Information Figures S1–S4), even though stem succulents are known from those regions (Eggli, 2004).

The near absence of stem succulents and any occurrences of the succulent biome from Australia is striking and well known, but poorly understood (Ellenberg, 1981; Holtum et al., 2016). Several introduced stem succulent cactus species have invaded large parts of Australia (Ellenberg, 1981; Holtum et al., 2016), indicating that stem succulents can thrive there, and our Old and New World models both predict large parts of Australia as climatically suitable for stem succulents (Supporting Information Figure S8). Our models thus disagree with Ellenberg's view that the climatic envelope of stem succulents in Africa and America is absent in Australia (Ellenberg,

1981; Holtum et al., 2016). It is possible that longer-term climatic oscillations exclude stem succulents from Australia, as the CHELSA climatic data used in this study only reflect the last c. 35 years (Karger et al., 2017). Alternatively, the deep history of fire in Australia (Crisp, Burrows, Cook, Thornhill, & Bowman, 2011) may have rendered the continent unsuitable for stem succulents throughout the Cenozoic, in line with the idea that most of northern and central Australia are assigned as grassy, fire-prone savanna (Lehmann et al., 2019). The absence of stem succulents from most of Asia is in line with the view that 'dry forests' in Asia are better regarded as savannas because they also have a flammable C_4 grass layer (Dexter et al., 2015; Lehmann et al., 2019; Ratnam et al., 2011).

4.3 | Succulent biome phylogenetic conservatism

We demonstrate high levels of phylogenetic succulent biome conservatism in a cohort of non-succulent plant clades that comprises prominent and in some cases dominant elements of this biome (Figure 3 and Table 1). This suggests that the succulent biome forms a tightly delineated evolutionary arena for drought-adapted plants. These patterns of succulent biome conservatism are especially striking given that many of the species are separated by large geographical (often trans-continental) disjunctions from their nearest relatives yet still occur within the succulent biome (Figure 3), suggesting that the high levels of biome conservatism are not simply the result of limited dispersal abilities. This confirms earlier results (Gagnon et al., 2019; Lavin et al., 2004; Thiv et al., 2011) and suggests that for lineages spanning the trans-continually distributed succulent biome it has been 'easier to move than to evolve' as highlighted by Donoghue (2008, 2019). This shows that the idea that local recruitment and independent origins of biomes within continents is a universal rule governing biomes in general (Pennington et al., 2018), clearly is not applicable to the succulent biome with its high levels of trans-continental phylogenetic conservatism.

Succulent biome phylogenetic conservatism, far from being restricted to legumes where it was first documented (Donoghue, 2019; Gagnon et al., 2019; Lavin et al., 2004), is prevalent across a range of plant families, and certain animal lineages (Supporting Information Table S5). These findings are comparable to some of the most striking examples of global phylogenetic biome conservatism (Crisp et al., 2009; Donoghue & Smith, 2004; Wiens & Donoghue, 2004), suggesting that phylogenetic conservatism may be most apparent at this broad biome level (Segovia et al., 2019). Furthermore, our results benefit from the additional rigour that comes from a quantitative biome model and use of detailed species occurrence data to objectively and quantitatively assign species to biomes.

4.4 | Biomes as evolutionary arenas

We show that the succulent biome shows striking convergence of functional traits [in stem succulence, early burst pre-rain leaf flushing (Donoghue, 2019; Gagnon et al., 2019; Oliveira-Filho et al., 2013)

and spinescence (see below)], as well as high levels of phylogenetic succulent biome conservatism in 10 non-succulent clades (Table 1). In other words, the confluence of evolutionary convergence and phylogenetic biome conservatism strongly suggests the succulent biome forms a well-defined evolutionary arena (Gagnon et al., 2019; Lavin et al., 2004; Oliveira-Filho et al., 2013; Schrire et al., 2005; Thiv et al., 2011). However, current global biome maps do not recognize the succulent biome (e.g. Friedl et al., 2010; Higgins et al., 2016; Olson et al., 2001; but see Pennington et al., 2018), and it has received limited attention in recent years. This neglect of the succulent biome has far reaching implications for understanding tropical diversity.

For example, recognizing the succulent biome is important for understanding the origins of the savanna biome, especially in Africa. Charles-Dominique et al. (2016) argued that contemporaneous evolution of spinescence and diversification of bovids in the mid-Miocene underpinned the rise of African savannas. However, regions with high diversity of spiny plant species (their fig. 2b) and bovids (their fig. 2c and e) substantially overlap with the succulent biome (our Figure 1), rather than comprising savanna as suggested by Charles-Dominique et al. (2016), a view reinforced by the relative paucity of perennial grasses in these areas (Lehmann et al., 2019). Spinescent plants are prevalent across many plant lineages throughout the succulent biome (e.g. the 'Spiny Forest' of south-west Madagascar; see also Cowling et al., 2005; de Queiroz et al., 2017; Pérez-García et al., 2012), providing another example of evolutionary convergence of an important plant functional trait associated with this biome. It seems likely that initial diversification of spiny plant lineages somewhat earlier than the arrival of bovids in Africa, and well before the rise to dominance of C_4 grasses (Charles-Dominique et al., 2016: fig 4), could reflect, not the emergence of savannas, but rather the earlier evolution of spinescence in plant clades occupying the succulent biome, which is thought to pre-date the savanna biome (Gagnon et al., 2019).

It remains to be seen to what extent other global biomes constitute evolutionary arenas characterized by similar combinations of convergence and conservatism to those demonstrated here for the succulent biome. While the flora of the global savanna biome shows several examples of evolutionary convergence in fire-related traits such as geoxyles, there is little evidence of global phylogenetic savanna biome conservatism; instead, different parts of this biome were apparently assembled via repeated local or in situ recruitment and adaptation of lineages via biome shifts from geographically adjacent biomes within the same continent (Maurin et al., 2014; Moncrieff et al., 2014; Simon et al., 2009). The flora of the Mediterranean biome also displays a suite of convergent plant functional traits, and there are at least forty genera occurring in two or more of its regions suggesting some degree of trans-continental Mediterranean biome conservatism (although no genus is known from all five Mediterranean regions; Ackerly & Onstein, 2018). Whether these and other biomes constitute evolutionary arenas remains to be determined via more thorough, cross-continental comparisons and assessments of the degrees of

evolutionary convergence and phylogenetic biome conservatism (Corlett & Primack, 2006).

5 | CONCLUSIONS

We highlight the utility of the convergence of key plant functional traits for defining and mapping the little-known succulent biome. We show that this biome forms a tightly delineated geographically disjunct, trans-continental evolutionary arena for drought-adapted plant lineages, providing some of the strongest evidence to date that ecology has played a key role in dictating the geographical turnover of clades across the lowland tropics (Segovia et al., 2019). We suggest that the dichotomy between succulent-rich, grass-poor, fire-free and succulent-lacking, grass-dominated, fire-prone vegetation reflects a fundamental functional distinction underpinning recognition of two distinct non-forest tropical lowland biomes, both of which are 'open' vegetation formations with seasonally dry climates, and both of which are ancient and merit attention (Bond, 2005; Cowling et al., 2005; White, 1983). This is supported by the largely non-overlapping distributions of the succulent and savanna biomes, as depicted in Figure 1 and the most recent global map of grassy biomes (Lehmann et al., 2019). Such a division is also very much in line with broad division of the lowland tropics into three main biomes—rain forest, savanna and succulent (Dexter et al., 2018; Lavin et al., 2004; Pennington et al., 2018; Schrire et al., 2005)—rather than the two broad categories prevalent in many macroevolutionary and macroecological studies. Finally, we show that the confluence of evolutionary convergence and phylogenetic biome conservatism can provide a strong indication that geographically disjunct areas of the same biome form a single coherent evolutionary arena, suggesting that in-depth cross-continental comparisons of convergence and conservatism in other biomes would be worthwhile.

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DATA AVAILABILITY STATEMENT

A raster file of the succulent biome map, occurrence data of stem succulents and the study clades, and an R script for cleaning up occurrence data can be found on Dryad (doi:10.5061/dryad.08kpr4zs).

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BIOSKETCH

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the Supporting Information section.

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